BEETLES ASSOCIATED WITH SLIME MOLDS (MYCETOZOA) IN OREGON AND CALIFORNIA (COLEOPTERA: LEIODIDAE, SPHINDIDAE, LATHRIDIDAE)

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Although the slime molds (Mycetozoa, or Myxomycetes) are an abundant and remarkably isolated group of organisms (Olive, 1975), there has been little recognition in the American literature of a beetle faunule adapted to feed on mycetozoan fruiting structures. This omission is likely due to most entomologists being unfamiliar with slime molds, which are often minute and often resemble certain types of true Fungi. The present paper records 11 species of beetles found by the author in four genera of slime molds in Oregon, and two beetle species found in two slime molds in California. This "guild" is compared with previously reported beetle associates of mycetozoans, principally those compiled from the European literature by Benick (1952).

Beetles have been collected in the following mycetozoans: Fuligo septica (Gmelin) and Reticularia lycoperdon (Ehrenb.), both occurring as massive compound sporangia (aethalia), and Arcyria denudata (L.) and Stemonitis spp., which occur as dense and sometimes extensive patches of stalked sporangia. Lycogala epidendrum (L.) has been cited as a host for Sphindus spp. in Europe, but I have found no beetles in two collections of this puffball-like species (Benton County, Oregon). Andrews (1977) has given the only published records of North American beetles from Fuligo and Arcyria and I have seen no American records for Reticularia as a host. Only a few definite records are available for beetles from other mycetozoan genera (Table 1).

Collections of Fuligo from widely separated Oregon localities have yielded 10 beetle species: Sphindus crassulus Csy. and Odontosphindus clavicornis Csy. (Sphindidae); Enicmus cordatus Belon (Lathridiidae); Anisotoma confusa Horn, Anisotoma errans Brown, Anisotoma nevadensis Brown, Agathidium contiguum Fall, Agathidium pulchrum LeC., Agathidium brevisternum Fall, and Agathidium californicum Horn (Leiodidae). As many as three species of beetles have been found in a single aethalium. These collections include the first Oregon records for the family Sphindidae. (Collection records are listed separately below.)

Most of the Fuligo associated beetles were found in mature, dry aethalia,

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Table 1. Previously reported and new records of beetles associated with slime-molds.

Beetle	Beetle family	Slime mold ¹	Slime mold family ¹	Reference
1. Oxytelus tetracarinatus (Block)	Staphylinidae	Reticularia olivacea (Ehrenburg)	Reticulariidae	Benick (1952)
2. Xantholinus punctulatus Paykull	Staphylinidae	R. olivacea	Reticulariidae	Benick
3. Quedius cruentus (Olivier)	Staphylinidae	R. olivacea	Reticulariidae	Benick
4. Q. mesomelinus (Marsham)	Staphylinidae	R. olivacea	Reticulariidae	Benick
5. Philonthus fimetarius (Gravenhorst)	Staphylinidae	R. olivacea	Reticulariidae	Benick
6. Atheta amicula (Stephens)	Staphylinidae	R. olivacea	Reticulariidae	Benick
7. A. aterrima (Gravenhorst)	Staphylinidae	R. olivacea	Reticulariidae	Benick
8. A. fungicola (Thomson)	Staphylinidae	R. olivacea	Reticulariidae	Benick
9. A. inoptata (Sharp)	Staphylinidae	R. olivacea	Reticulariidae	Benick
10. A. oblita (Erichson)	Staphylinidae	R. olivacea	Reticulariidae	Benick
11. Bacanius rhombophorus Aube	Histeridae	Fuligo septica (Linne)	Physaridae	Benick
12. Agathidium confusum Bristol	Leiodidae	Reticularia lycoperdon (Bullard)	Reticulariidae	Benick
13. A. rhinoceros Sharp	Leiodidae	R. lycoperdon	Reticulariidae	Benick
14. A. seminulum (Linne)	Leiodidae	Arcyria denudata (Linne)	Trichiidae	Benick
		Fuligo septica	Physaridae	Benick
		Reticularia lycoperdon	Reticulariidae	Benick
15. A. sphaerula Reitter	Leiodidae	Arcyria denudata²	Trichiidae	Benick
•		Reticularia lycoperdon	Reticulariidae	Benick
16. A. pulchrum LeConte	Leiodidae	Stemonitis sp.	Stemonitidae	Hatch (1957)
		Fuligo septica	Physaridae	PRESENT PAPER
		Arcyria denudata	Trichiidae	PRESENT

Table 1. Continued.

Beetle	Beetle family	Slime mold ¹	Slime mold family ¹	Reference
17. A. rotundulum Mannerheim	Leiodidae	A. denudata	Trichiidae	PRESENT
18. A. californicum Horn	Leiodidae	Fuligo septica	Physaridae	PRESENT
19. A. brevisternum Fall	Leiodidae	F. septica	Physaridae	PRESENT
20. A. contiguum Fall	Leiodidae	F. septica	Physaridae	PRESENT
21. Amphicyllis globiformis Sahlberg	Leiodidae	slime mold	?	Benick
22. Anisotoma axillaris Gyllenhal	Leiodidae	Reticularia lycoperdon	Reticulariidae	Benick
23. A. castanea Herbst	Leiodidae	R. lycoperdon	Reticulariidae	Benick
		Fuligo septica	Physaridae	Benick
24. A. glabra Kugel	Leiodidae	slime mold	?	Benick
25. A. humeralis Fabricius	Leiodidae	Reticularia lycoperdon	Reticulariidae	Benick
26. A. orbicularis Herbst	Leiodidae	R. lycoperdon	Reticulariidae	Benick
27. A. confusa Horn	Leiodidae	Fuligo septica	Physaridae	PRESENT
28. A. errans Brown	Leiodidae	F. septica	Physaridae	PRESENT
29. A. nevadensis Brown	Leiodidae	F. septica	Physaridae	PRESENT
30. Thymalus limbatus (Fabricius)	Ostomidae	Reticularia lycoperdon	Reticulariidae	Benick
31. Reveliera californica Fall	Lathridiidae	Arcyria versicolor Phillips	Trichiidae	Andrews (1977)
32. Enicmus cordatus Belon	Lathridiidae	Fuligo septica	Physaridae	PRESENT
		Stemonitis sp.	Stemonitidae	Hatch, PRESENT
33. E. tenuicornis LeConte	Lathridiidae	Stemonitis axifera (Bullard)	Stemonitidae	PRESENT
34. E. fungicola Thomson	Lathridiidae	Reticularia lycoperdon	Reticulariidae	Benick
35. E. rugosus (Herbst)	Lathridiidae	Fuligo septica	Physaridae	Benick
		Reticularia lycoperdon	Reticulariidae	Benick

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Table 1. Continued.

Beetle	Beetle family	Slime mold ¹	Slime mold family ¹	Reference
36. E. testaceus (Stephens)	Lathridiidae	R. lycoperdon	Reticulariidae	Benick
37. C. consimilis (Mannerheim)	Lathridiidae	slime mold	?	Benick
38. E. hirtus Gyllenhal	Lathridiidae	slime mold	?	Benick
39. E. minutus (Linne)	Lathridiidae	slime mold	?	Benick
40. Lathridius nodifer Westwood	Lathridiidae	slime mold	?	Benick
41. Aspidophorus lareyniei Duval	Sphindidae	slime mold	?	Benick
42. A. orbiculatis Gyllenhal	Sphindidae	Reticularia lycoperdon	Reticulariidae	Benick
43. Odontosphindus clavicornis	Sphindidae	Fuligo septica	Physaridae	Andrews, PRESENT
Casey		Stemonitis sp.	Stemonitidae	Hatch (1962)
44. O. denticollis (LeConte)	Sphindidae	slime mold (?)	?	Frost (1947) ³
45. Sphindus crassulus Casey	Sphindidae	Fuligo septica	Physaridae	PRESENT
46. S. dubius Gyllenhal	Sphindidae	Lycogala epidendrum (Linne)	Liceidae	Benick
		Fuligo septica	Physaridae	Benick
		Reticularia lycoperdon	Reticulariidae	Benick
47. S. grandis Hampe	Sphindidae	slime mold	?	Benick
	•	Lycogala sp.	Liceidae	Crowson (1955)

¹ The nomenclature used is after Martin and Alexopoulos (1969), but names are given according to zoological usage, as in Olive (1975).

² Benick gives this host as Trichia cinnabara, a synonym of Arcyria denudata (Martin and Alexopoulos, 1969).

³ Frost does not cite this as a slime mold; this interpretation is highly likely from his description.

but the *Anisotoma* species have been taken more frequently in moist specimens which were transforming from the plasmodial phase. The lathridiids and sphindids were found throughout the powdery spore-bearing tissue of aethalia which varied in size from 3 cm to 10–15 cm diameter. The *Fuligo* specimens lacked evident entrance holes, which suggests that most of the beetles had developed *in situ*. Two lathridiid larvae were found with *E. cordatus* in 1 sample of *Fuligo*, and larvae and pupae of *O. clavicornis* were dissected from another *Fuligo* specimen. No insects other than the beetles mentioned were observed in any samples of *F. septica*.

Stemonitis spp. have also yielded both adults and larvae of Enicmus. Twenty-two adult E. tenuicornis LeC. were collected from a 3 cm wide patch of Stemonitis axifera (Bull.) under loose bark of a Lithocarpus log in Amador County, California. Several larvae were found with the adult E. tenuicornis and two were reared to the adult stage. Many E. cordatus were taken from a Stemonitis (species indet.) under oak bark in Benton County, Oregon.

A large collection of Arcyria denudata (L.) found on the Oregon coast in November, yielded adults of Agathidium pulchrum LeC. and Agathidium rotundulum Mann., as well as Agathidium larvae on and among the sporangia. Two Agathidium rotundulum adults were reared from larvae in this collection. A second collection of Arcyria denudata from near San Bernardino, California contained three adult Agathadium pulchrum.

Of the 12 beetle species listed above, only Agathidium pulchrum is known to be a general fungivore; I have found adults and larvae of this species in Oregon on the "oyster mushroom," Pleurotus ostreatus group, and on a jelly fungus, Tremella mesenterica (S. F. Gray) Pers., both of which are Basidiomycetes. I have also seen a specimen of Agathidium pulchrum labelled "on slime mold plasmodium" from King County, Washington (D.V. McCorkle, collector). Enicmus cordatus has been recorded from Neotoma nest, under bark, and in willow duff (Hatch, 1962), but it is my view (supported by F. G. Andrews, personal communication) that Mycetozoa are the usual breeding substrate for this species and perhaps for all *Enicmus* species in western North America. Odontosphindus clavicornis has been collected from the slime mold Stemonitis sp. in British Columbia (Hatch, 1962), and Andrews (1977) also records it from Arcyria versicolor Phill. and F. septica in California; no useful host records are available for the other beetle species above. Agathidium rotundulum and Agathidium brevisternum are relatively abundant in Berlese extracts from forest litter and may also be general fungivores; since Anisotoma spp. and the sphindids are rarely encountered except in flight (including light-trap collections), their occurrence in mycetozoans as reported here is likely to be obligatory. All the beetles listed here are related to beetles in Europe which are indicated as slime mold specialists (Benick, 1952).

Comparison with Known Insect Associates of Mycetozoa

The only available faunal area to compare with these West Coast slime mold beetles is Europe. There, as in North America, the best-documented association of a beetle taxon with Mycetozoa is for the Sphindidae. Benick (1952) lists four species of *Sphindus* and *Aspidophorus* from mycetozoans of the genera *Lycogala* and *Reticularia* (but also, less frequently from a few polypore and agaric fungi among the Basidiomycetes). Crowson (1955) stated that both British genera (*Sphindus*, *Aspidophorus*) "as far as known, feed exclusively on Mycetozoa."

In contrast, most American authors have characterized the Sphindidae as "dry-fungus beetles." Arnett (1963) for instance, indicates their habitat as being "in dry fungi, mostly shelf fungi on tree trunks and old logs." Aside from Hatch's (1962) record of Odontosphindus clavicornis on the slime mold Stemonitis, the only interpretable American host records for sphindids are those of Frost (1947) of Sphindus americanus in association with cisid species on "small, crowded, woody fungi," which may be the basidiomycete Polyporus versicolor or a similar species, and of Odontosphindus denticollis (LeC.) (as Eurysphindus denticollis) in a "flat, brown fungus of a soft smut-like consistency." The latter description is rather obviously of a mycetozoan. The usual occurrence of O. clavicornis in slime molds, and my single record of Sphindus crassulus in Fuligo further increase the probability that this host association is usual, if not exclusive, in the Sphindidae. While observations of sphindids apparently feeding on polypore fungi cannot be completely discounted, they may have been confounded by the frequent occurrence of mycetozoan plasmodia in old polypore sporocarps (Martin and Alexopoulos, 1969). The common application of the term "polypore" to almost any dry or woody sporocarp also makes acceptance of such records questionable.

The other genera of beetles reported here from slime molds are also probable mycetozoan specialists. All of the seven species of *Anisotoma* and six species of *Enicmus* in Benick's list of European mycophagous beetles have been reported from slime molds. In most cases this is the usual or exclusive substrate, although *Enicmus* species are rather often cited from hosts among the true Fungi. Benick also reported four of 19 listed species of *Agathidium* from slime molds; the host restrictions in this genus vary at the species level. Of the European beetle genera commonly cited from mycetozoan hosts, only *Amphicyllis* (Leiodidae) is missing from my collections; this genus does not occur in North America.

Although I found different species on Fuligo and on Arcyria, there is no good evidence of specialization on particular mycetozoan hosts. In part I have observed a seasonal effect, for Enicmus and the Sphindidae are evidently adapted to very xeric conditions, while the Leiodidae require more moisture, and are (in the Pacific Northwest) more typically active in cool,

moist weather. The aethalia containing *Anisotoma* and *Agathidium* were usually located in moist sites under bark or on the surface in deep shade, while *Enicmus* and *Odontosphindus* were often found in very exposed sites. The mycetozoans listed as hosts in Table 1 belong to four of the five orders of Myxogastria (the true slime molds) recognized by Oliver (1975); it is likely that all slime mold sporangia of sufficient size are subject to attack by beetles.

It is probable that most or all of the Coleoptera specializing on myceto-zoans feed on the spores; Andrews (1977) has found this to be the case for the lathridiid *Reveliera californica* Fall. The basis for the differentiation of Mycetozoa as a coleopteran food-niche may be nutritional, or be related to the rapid desiccation of the slime mold. The slime mold fauna is clearly derived from mycophagous taxa, even though the Mycetozoa are best regarded as colonial Protozoa not directly related to the true Fungi (Olive, 1975). It is interesting to note that this speciality can be observed among the Coleoptera at the family (Sphindidae), genus (*Anisotoma*, *Enicmus*), and species (*Agathidium*, in part) taxonomic levels.

Aside from beetles the Diptera appear to be the only important insect associates of slime molds. Buxton (1954) bred 16 species of flies, representing 10 families, from mycetozoans. These included several apparent slime mold specialists, as well as a number of common saprozoic species which feed on rotting plasmodia. The absence of fly-infested material from my collections presumably accounts for the lack of predatory, mycetophilous staphylinids in my list, in contrast to those cited by Benick (1952).

Collection Data

Fuligo septica (Gmelin)

Oregon: Benton County. a) MacDonald State Forest, VII-18-75, Loren Russell Collector. 1 aethalium on Douglas fir stump: *Odontosphindus clavicornis* Csy. (10 specimens), *Sphindus crassulus* Csy. (1), *Enicmus cordatus* Bel. (14). Many beetles escaped. b) Marys Peak, 610 m elevation, V-8-77, Loren Russell. 1 aethalium on small branch: *Anisotoma errans* Brown (5). c) Marys Peak, 610 m, V-3-88, Loren Russell. 1 moist aethalium on stump. *Agathidium pulchrum* LeConte (1), *Agathidium brevisternum* Fall (1).

Marion County. Mt. Jefferson Wilderness Area, 10 km SE Breitenbush Hot Springs, 600 m, VIII-24-75, Bill Frost. 1 moist aethalium on Douglas fir stump: *Anisotoma confusa* Horn (12).

Jefferson County. a) 8 km N Suttle Lake, 930 m, VIII-9-75, Loren Russell. 3 aethalia on ponderosa pine litter on old log: O. clavicornis (38 adults, 5 pupae, 2 larvae), E. cordatus (3), Anisotoma errans Brown (2). b) Metolius River area, 900–950 m, V-28-76, Loren Russell and P. J. Johnson. Aethalia under bark of ponderosa pine stumps: O. clavicornis (7), E. cordatus (3),

Anisotoma confusa (4). c) Dark Lake, IX-14-77, G. L. Peters. Several aethalia. O. clavicornis (1), E. cordatus (5), Agathidium contiguum Fall (47), unidentified leiodid (2).

Crook County. Bandit Springs Wayside, 1 km SW Ochoco Summit, 1380 m, V-29-76, P. J. Johnson. 1 aethalium under pine bark: *Anisotoma confusa* (2), *Agathidium californicum* Horn (1).

Wheeler County, Ochoco Divide Campground, 1350 m, VII-16-77, Loren Russell. 2 fresh aethalia on Douglas fir log: *Anisotoma nevadensis* Brown (14), *Agathidium contiguum* (4), *O. clavicornis* (43).

Klamath County. Lake of the Woods, 1500 m, VII-20-75, Loren Russell. 5 small aethalia on pine litter: *E. cordatus* (34).

Reticularia lycoperdon (Ehrenb.)

Oregon: Crook County. Maury Mtns., Drake Butte, 1890 m, VII-25-76, Loren Russell. 1 old eroded aethalium, 1 fresh aethalium on cut surface of pine stump: *E. cordatus* (18).

Arcyria denudata (L.)

Oregon: Tillamook County. Cascade Head, Nature Conservancy Trail, XI-21-75, Loren Russell. One 30×5 cm patch of eroded sporangia on side of red alder log: $Agathidium\ pulchrum\ (3)$, $Agathidium\ rotundulum\ Mannerheim\ (1\ adult,\ 2\ others\ reared\ from\ larvae\ on\ this\ sample)$.

Linn County. 5 km SE Jordan, VII-2-77, Loren Russell. In moist cavity of rotted maple stump: Agathidium pulchrum (7).

California: Los Angeles County. Mt. San Antonio, IV-27-76, Loren Russell. Small patch of sporangia on log buried in river bar: *Agathidium pulchrum* (3).

Stemonitis axifera (Bull.)

California: Amador County. 2 km E Jackson, V-4-76, Loren Russell. 3 cm patch of sporangia under loose bark of *Lithocarpus*: *Enicmus tenuicornis* LeConte (22 adults, several larvae).

Stemonitis sp. indet.

Oregon: Benton County. a) MacDonald State Forest, VIII-21-76, G. L. Peters. Under bark of oak log: *E. cordatus* (18). b) Same locality and host, VI-26-77 Loren Russell *E. cordatus* (3).

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